

4 Aggregation responses of soil arthropods in relation to the soil environment*

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Summary

The majority of field studies of Collembola and Acarina have shown that aggregations are a common feature of the distribution of these arthropods. In attempting to find the cause of these aggregations, the use of the correlation coefficient between the number of arthropods and measures of the physical environment is problematical since cause and effect cannot be established from the significance or otherwise of this coefficient. In controlled laboratory environments the location of a food source tends to be of importance in determining the site if not the size of an aggregation.

Data are presented for a Scots pine (*Pinus sylvestris*) forest soil in Perthshire, Scotland. Areas of high nutrient status have different size dimensions. Aggregated distributions of arthropods are frequent, and these are divided somewhat subjectively into large (gradients) and small (distinct) aggregations. In general, it will be shown that predatory species are less strongly aggregated than detritus and fungus feeders. The distinct aggregations can be uniformly or randomly distributed or aggregated themselves. It is shown that in some species more aggregations are formed at higher population densities, whilst in other species the number of arthropods per aggregation increases with population density. The whole community is analysed by

*In order to avoid confusion over the use of the word 'Factor' in several different contexts, the following convention has been used in this paper:

'Factor' has been retained for any one of the mathematical abstractions derived from a 'factor analysis' of the data.

'Feature' has been used in the context usually covered by 'environmental factor', i.e. environmental features are individually measured components of the environment.

'Influence' has been used in the context usually covered by 'the factor affecting sp. A was ...', where in this paper such a sentence would be written 'the influence affecting sp. A was ...'.

both principal component and factor analyses. The results of these two methods are not particularly different, though rotation of the axes in a factor analysis might assist in the biological interpretation. The general conclusion that can be drawn from these analyses is that the most important effect on the arthropod community is structural, a combination of depth in the soil, soil water content and pore space, but that these influences are so closely correlated that their individual effects, if any, are inseparable.

There is a discussion of aggregation in soil arthropods and pattern in plant communities. The causes of both are complex and may relate to the establishment of a larger population density than in an unaggregated population. The comparative stability of the soil environment may contribute to its species richness.

Introduction

The majority of studies on the arthropods which live in litter or soil have shown a nonrandom distribution, with the arthropods occurring together in small localized pockets of high density. Such a feature of animal distributions has usually been termed 'aggregation': the word 'aggregate' is defined by the Oxford English Dictionary as 'collect together' and seems to imply some active process on the part of the individuals. The word 'pattern' has been used to describe nonrandomness in plant distributions: this word tends to imply a passive, or certainly less active, process generating the nonrandomness. The two words do, however, describe the same phenomenon: the occurrence together in a few localized areas of more organisms than would be expected if the organisms were distributed at random.

Field studies in relation to aggregation behaviour of soil arthropods tend to have had one of three aims. First, some studies seem content to demonstrate aggregation. That aggregations exist has now been demonstrated for so many species that there is no need to list the species. Secondly, aggregation imposes statistical problems on sampling—how many samples are needed to give an accurate estimate of the mean population density, or what is the underlying probability distribution so that an efficient transformation can be carried out to normalize the data before applying tests of significance? It has been shown that the negative binomial distribution often gives a good fit to data consisting of counts of mites and Collembola (Nef 1962; Berthet & Gérard 1965), though Hartenstein (1961) obtained a better fit with the Neyman A distribution for some species. Thirdly, some studies have endeavoured to determine the causes of aggregations.

Perhaps the most important environmental influence acting upon the soil arthropods is the soil water. Hale (1967) considers that the Collembola,

whilst not in general indicating soil conditions, might reflect the water content of soils. Several studies have shown positive correlations between soil water content and the numbers of arthropods in forest soils. Poole (1961, 1962) has demonstrated such a relation for the Collembola *Friesea mirabilis*, *Tullbergia krausbaueri*, *Megalothorax minimus* and *Isotoma notabilis* (some of these relations are based on correlation coefficients, others on partial correlation coefficients after elimination of such environmental features as the dry weight or depth of the organic matter). *Hypogastrura viatica* actively aggregates in places of high humidity (van der Kraan 1971). Lebrun (1971) has shown a positive correlation between soil water content and the logarithm of the numbers of some of the Cryptostigmata that he studied. Lebrun (1969) also suggested that the population density of *Nothrus palustris* was positively related to soil water content. In an old field ecosystem, Knight & Read (1969) have suggested that an optimum soil water content, 10–20% of dry weight, exists for maximum density of six species of *Tomocerus*. Some contrary results have been found in salt marshes, where Luxton (1967a) has shown that the total Cryptostigmata and total Mesostigmata are negatively correlated with water content (due both to tide and precipitation), though in a Puccinellietum soil he found no correlation between any group of mites and water content (Luxton 1967b). Joosse (1966) observed that the maritime Collembola *Anurida maritima* was stimulated to aggregate in cavities by the incoming tide or by rainfall during low water. Water, in excess, can also cause aggregations: van der Kraan (1971) has shown that *Hypogastrura viatica* is drifted into large aggregations with densities reaching 1,000 cm⁻² when it is floating on flood water.

Three theoretical features of the relation between soil water and arthropod distribution are of interest. First, Vannier (1970) has been concerned with pF thresholds acting as a stimulus for arthropods to move under desiccating conditions. He has shown (Vannier 1967) that at about pF 5 the Isotomidae respond more quickly than the Cryptostigmata. Secondly, Gifford (1968) has been concerned with the precise nature of the relation: whether soil water is in the form of vapour or liquid, and the water relations of the arthropod species (i.e. their cuticle structure, respiration and their ability to live in a water film). Thirdly, Joosse (1970, 1971) and Joosse & Verhoef (1974) have developed a theory that Collembola come together by undirected movements into small areas of optimum humidity conditions. They suggest that the formation of aggregations is significant since moulting and egg laying occur in these localized areas, and the greater population density increases the probability that the opposite sexes will be near each other for fertilization. It is suggested that the species of Collembola which aggregate most strongly are those with no courtship behaviour.

Local variation in temperature can also affect the distribution of soil

arthropods. Edwards & Lofty (1971) experimented by artificially heating soil, but since the heated plot was drier, there is likely to be an interaction between temperature and water content in these experiments. Lebrun & van Ruymbeke (1971) suggest that, since development time in Cryptostigmata is related to temperature, the maximum population density of *Damaeus* sp. occurs in sites with an optimal temperature. The data for cold temperatures are somewhat conflicting. Whilst Healey (1967) observed activity at -6°C and feeding and defaecation at -4°C in *Onychiurus procampatus* in environments in which the temperature had dropped slowly, he also showed that sudden drops in temperature to 5°C could render the animals inactive. Tillbrook (1967) considered that the pattern of distribution of antarctic arthropods could result from winter deaths due to cold, whilst Remmert & Wisniewski (1970) have shown that Collembola are resistant for several hours to subzero temperatures during the arctic summer.

Temperature might be the influence causing aggregations of *Isotoma viridis* and various species of mites under white as opposed to black boards (Jensen & Corbin 1966), though it is suggested that time of day, past weather and humidity are also responsible for these aggregations. Jensen (1968) later showed that white boards do attract more species of Collembola than black boards. Schalk (1968), discussing the physical structure of the environment, has shown that there are larger populations of arthropods in sandy than in loamy areas, and Haarlov (1960) has illustrated relations between pore structure and arthropod size. There is some evidence, however, that Collembola can modify the structure of their environment by building cells of faecal material (Poinot 1966; Massoud *et al.* 1968). Poole (1961, 1962) has shown that many species of Collembola are positively correlated with the depth of the organic layer in coniferous forest soils. Luxton (1967b) shows negative correlations between all groups of mites and pH in saltmarsh soils, whereas Wakerley (1963) found an optimum pH for Collembola density in grassland plots at pH 6.5. He also showed that the density of Collembola increased linearly with phosphate content of the soil, and thus that maximum population density occurred under conditions of high phosphate at pH 6.5, the conditions required for a good grass sward. Edwards & Lofty (1969), however, found that an increase in pH increased the population density of some species, and decreased the density of other species. They also found that whereas inorganic fertilizers slightly increased the population densities of both mites and Collembola, organic fertilizers more than doubled the populations of both groups. This result is in accord with Gisin (1955) who found that organic manure increased the populations of all Collembola in vineyard soils.

These studies, based on field data, would indicate that the physical and chemical environment of the soil have a particularly strong effect on the

location of aggregations. However, laboratory studies with *Pseudosinella impediens* (Christiansen 1970; Barra & Christiansen 1975), *Hypogastrura bengtssoni*, *Proisotoma minuta*, *Folsomia candida* and *Sinella coeca* (von Törne 1974) and *F. candida* (Usher & Hider 1975) have all shown that the location of a food source is the most important influence determining the site of an aggregation. The studies on *P. impediens* show that food as an influence is more important to the young stages than to the adults. The studies on *F. candida* have shown that water is also an important influence.

Although food can be measured in laboratory studies, it is a feature that is difficult to measure in the field. Results or reviews on the feeding habits of Mesostigmata are given by Karg (1961), Cryptostigmata by Wallwork (1958) and Hartenstein (1962), mites generally by Wallwork (1967), and Collembola by Poole (1959), Bødvarsson (1970) and Petersen (1971). In general these studies show that soil arthropods are not very specific feeders. However, laboratory studies have shown that there are preferred foods, particularly with fungus-feeding species. Thus, *Nothrus biciliatus* preferred one out of 17 fungi offered to it, and in general it found young fungal cultures more attractive than old ones (Saichuae *et al.* 1972). Mills & Sinha (1971) found that *Hypogastrura tullbergi* showed a preference for four out of 43 fungi and actinomycetes. These four species were characterized by forming a mycelial mat which permitted free movement of the Collembola. The generality of feeding, shown by field studies, can be partly explained by lack of availability of the preferred food: thus in the laboratory Knight & Angel (1967) found *Tomocerus* predominantly fed on fungal spores, eating rather little litter, humus or fungal hyphae, whilst in the field where spores were scarce the species ate more litter and fungal hyphae. Despite the observed generality of feeding, it is thus possible that aggregations are located where there are particularly favoured fungi, etc.

Preference for certain species of microflora might also be responsible for the succession of arthropods on decaying vegetable material. Winston (1956) has described the succession of arthropods on decomposing acorns, whilst Hayes (1963) has shown that some Phthiracarid mites occur at an earlier stage of the decomposition of coniferous needles than other species. The spatial arrangement of acorns or needles would thus be capable of determining the aggregation patterns of species. Pande & Berthet (1973) show that whilst *Phthiracarus* spp. are more usually associated with twigs in the litter, *Microtritia minima* is more usually associated with needles and *Rhysotritia duplicata* with bark, though the three species are not confined to these preferred components of the litter. A positive correlation between the roots of *Artemisia campestris* and *Rhysotritia* (*Pseudotritia*) *ardua* has been found in the field by Führer (1961), who also demonstrated this relation in laboratory experiments with water extracts of dead and decaying *Artemisia* roots.

Curry (1973) has shown that species of *Isotoma* can select litter of various plant species under field conditions: *I. notabilis* is most frequent in *Dactylis glomerata* litter and *I. viridis* in *Rumex crispus* litter. Bagnall (1932) recorded *Sminthurinus cingulatus* in Norway and Britain only around *Pedicularis palustris* plants. Blackith (1974) suggests that aggregations are formed in the rhizosphere of the favoured higher plant.

Besides the food and environmental influences acting to cause aggregations, there would also appear to be some inbuilt sociability in the arthropods themselves. Some of this might result from egg clusters since juveniles are frequently aggregated (e.g. *Folsomia quadrioculata* juveniles, Macfadyen 1952). Joosse (1970, 1971) and Joosse & Verhoef (1974) have suggested that the formation of aggregations is important in the moulting process, as well as being a replacement for courtship behaviour prior to egg laying. Wallace (1967) has shown that at high density the newly hatched nymphs of *Sminthurus viridis* eat dead and dying adults, in which there are large quantities of uric acid, and die. He suggests that this is density-dependent mortality. It might be appropriate to speculate that some means of population control is achieved through the formation of aggregations. There is some evidence to suggest that aggregations are multispecific in content. Poole (1961) has suggested this in the Collembola of a coniferous forest soil, and Gridelet & Lebrun (1973) have demonstrated a positive correlation between *Dermatophagoides pteronyssinus* and *Cheyletus* sp. However, the mechanism for the existence of several species in the same aggregation is difficult to explain. Laboratory experiments by Christiansen (1967) and Longstaff (1974) have demonstrated the difficulty of maintaining cultures of two or more species of Collembola.

Aggregations would therefore appear to be caused by a variety of influences. Perhaps the most important of these is the location of favoured food sources, though soil moisture is also likely to be of importance. The correlation between food and water under field conditions is unknown, and hence field data suggesting water and laboratory data suggesting food may be manifestations of the same influence, i.e. that the preferred food grows best at some particular water content. The causes of aggregations under field conditions are analysed in the remainder of this paper. The sampling scheme was designed to provide information on a number of these possible influences acting to cause aggregations, in relation to both the chemical and physical environment in which the arthropods were living. It was, however, impossible to investigate the local distribution of food sources since the preferences of each species were unknown and since the small soil sample was destroyed during the extraction of the arthropods and the analysis of the physical and chemical environment.

THE PHYSICAL AND CHEMICAL ENVIRONMENT

Site factors

The data relate to a sampling site, approximately 20 m square, on Cnoc Eòghainn, a southerly outlyer of the Black Wood of Rannoch in Perthshire, Scotland ($56^{\circ} 40' \text{N}$, $4^{\circ} 22' \text{W}$; National Grid Reference NN551546). The cnoc is at an elevation of approximately 380 m, and is covered with a stand of pine trees, *Pinus sylvestris* L. ssp. *scotica* (Schott) E.F. Warburg, which were mostly 80 to 90 years old. The ground is not wholly covered with herbaceous vegetation due to winter grazing by sheep and deer (a small fenced enclosure on the cnoc quickly became fully vegetated). The most frequent herbaceous species are wavy hair-grass, *Deschampsia flexuosa* (L.) Trin., heath bedstraw, *Galium hercynicum* Weigel and wood-sorrel, *Oxalis acetosella* L. The sparseness and uniformity of this ground flora considerably eased the problems of sampling the soil fauna. The climate is cold and moist, with an annual precipitation of approximately 118 cm and a mean annual temperature of 6°C (the mean temperatures for January and February are close to 0°C). The soil is a humus iron podsol, which has a litter horizon about 5 mm deep (where no drifting of litter has occurred), a fermentation horizon of approxi-

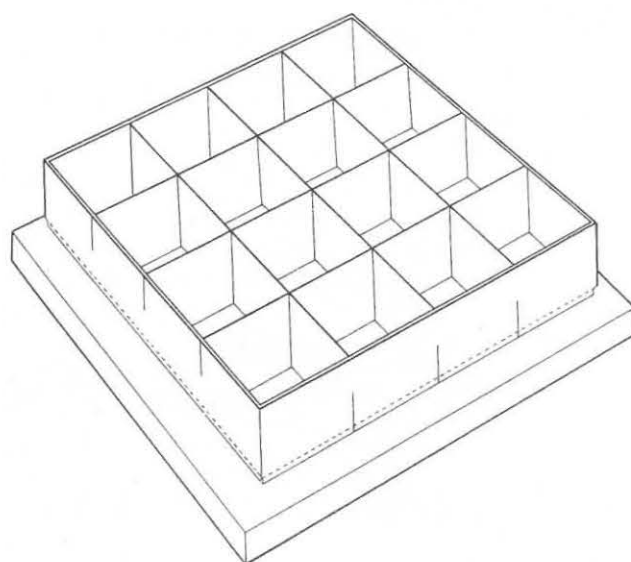


Figure 4.1. The sampling tool used to cut sixteen contiguous, square soil cores. The tool was constructed of stainless steel blades which were hollow ground to facilitate sharpening. Each core was divided into three horizontal layers, each 1 cm thick, before extraction of the arthropods and measurement of the environment features.

mately 10 cm depth, and a humus horizon of approximately 28 cm depth. Stones are absent in the organic horizons.

Blocks of 16 contiguous square soil cores, arranged in a square four cores by four cores, were cut with a sampling tool (see Fig. 4.1) to a depth of 3 cm. Thus, this study concentrates on the arthropods and environment of the litter and upper fermentation horizons (extraction from deeper cores indicated that approximately 95% of the arthropods occurred in the surface 3 cm). Each core was 4 cm square, and was divided into three layers, each of 1 cm thickness. The sampling tool thus yield 48 soil samples; the location of this block of samples being randomly selected within the sampling area.

Horizontal distribution in the soil

Two physical features (soil water content and soil pore space) and four chemical features (nitrogen, phosphorus, potassium and calcium concentrations) were measured in all 1,152 samples that were collected. The techniques of analysis of these samples have been described by Usher (1970a). Although a seasonal distribution or longer term trends were observed for these environmental features, they also showed characteristic horizontal distributions.

The water content of two blocks of samples, one taken in December at the time of greatest mean water content and the other taken in July at the time of least water content, are shown in Fig. 4.2. In the December data,

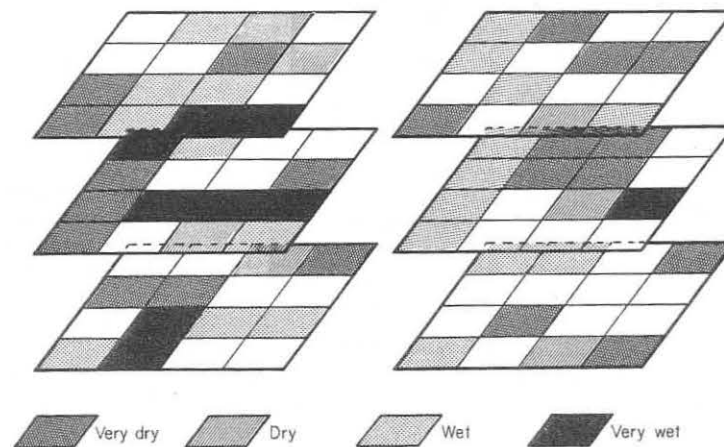


Figure 4.2. The distribution of wet and dry samples in two blocks of samples collected in December (left—the time of the greatest water content) and in July (right—the time of the least water content).

the mean water content of the surface, expressed as weight of water to oven dry weight of soil, is 257% (95% confidence limits are 238–276%). Samples with below 238% water content have been designated 'dry', and samples with above 276% as 'wet'. Similarly, dry and wet samples have been designated with respect to the mean for each other layer. It can be seen in Fig. 4.2 that there is considerable variability in the surface and centre layers, with the wet and dry samples being more or less randomly arranged, though there are strong vertical similarities between the two layers. In the lowest layer the wet and dry samples are not randomly arranged, but show moisture gradients, probably due to the greater environmental stability of this layer. The pore space showed no definite horizontal distribution. Vertically, pore space showed a distinct distribution, being greatest in the surface layer.

All four nutrients showed some degree of heterogeneity in their distributions. The nitrogen distribution in all seasons of the year typically shows samples with high or low nitrogen concentration randomly distributed. Since high nitrogen occurs in single samples or pairs of samples, it can be seen that the 'concentration aggregation' of nitrogen occupies a volume of 16–32 cm³. These 'concentration aggregations' of nitrogen are the smallest observed at Rannoch. The three other nutrients measured also formed 'concentration aggregations', but of a larger volume. Such 'concentration aggregations' for potassium occupy a horizontal area of 32–64 cm², and vertically they are reflected to a depth of at least 3 cm. Thus the volume of these 'concentration aggregations' is of the order of 100–200 cm³. Phosphorus occurred in the blocks of samples as a gradient running from areas of high to low phosphorus concentration. Such 'concentration aggregations' are approaching the volume of the whole block of samples, and thus they are of the order of 750 cm³ in volume. There is no season of the year when the distribution of calcium can be considered homogeneous. Calcium distribution can be in the form of small patches of high concentration, these patches being the same size or a little larger than the patches of high potassium concentration. Also, gradients of calcium concentration can be seen across some of the blocks of samples resembling the gradients of phosphorus concentration. Neither of these types of 'concentration aggregation' are found at any particular season of the year, and thus it would appear that the 'concentration aggregations' of calcium are more variable in volume than those of nitrogen, potassium or phosphorus.

Soil arthropods are thus faced not with a uniform soil environment, but with an extremely heterogeneous environment. A vertical distribution of environmental features could be predicted since the horizons change from litter to fermentation, and the deeper in the fermentation layer the longer the time lag between the litter falling and that stage of decomposition. However, there is an extremely heterogeneous horizontal distribution of environmental

features, these environmental features only being weakly correlated one with the other.

THE ARTHROPODS (COLLEMBOLA AND ACARINA)

When considering the distribution of individuals within the soil environment, three separate distributions can be considered, namely seasonal, vertical and horizontal. In relation to the formation of aggregations, the horizontal distribution is of greatest importance, though the vertical distribution of the arthropods can affect the distances between the centres of aggregations. Seasonal distribution is probably more closely related to the microclimate, though it must be remembered that as the population density changes so might the aggregation responses of the species. The seasonal and vertical distribution of the Collembola (Usher 1970b), of the Mesostigmata (Usher 1971b) and of the Cryptostigmata (Usher 1975a) have already been described.

If a series of independent samples of an insect population is available, Taylor (1961) showed that there was a relation between the sample variances and the sample means of the form

$$s^2 = a m^b \quad (4.1)$$

where s^2 is the sample variance, m the sample mean, and a and b are constants. Two facts emerge from equation 4.1. First, simple logarithmic transformation of both sides implies that the coefficients a and b can be estimated by regression analysis. Secondly, the coefficient b can be used as a measure of the aggregating tendency of the species (if a species is distributed according to the Poisson distribution then $b=1$). Since a total of 24 blocks of samples were collected for each of which a sample mean and a sample variance was calculated, the coefficients of equation 4.1 have been estimated. These have previously been described for the Mesostigmata (Usher 1971a) and the Cryptostigmata (Usher 1975b) and are listed for the Collembola in Table 4.1. In this table the values of the correlation coefficient are all large and significant, indicating that the relation in equation 4.1 generally fits the Collembola data well.

In order to compare the various groups of arthropods, data for the most frequent species are given in Table 4.2. The values of b are usually large (in excess of about 1.4) for the species of Collembola and Cryptostigmata. An exception to this is *F. quadrioculata*, but Usher (1969) has found that this is the only species of Collembola ever to show a uniform (regular) distribution in the soil. The values of b for the Mesostigmata are usually closer to unity and are probably related to the feeding habits of the Mesostigmata.

Table 4.1. The parameters of equation 4.1, where a and b have been estimated by regression analysis. The value of the correlation coefficient, r , between the logarithm of s^2 and the logarithm of m is given with the sample size in brackets.

Species	a	b	r	
<i>Anurida granaria</i> (Nicolet)	2.345	1.258	0.983	(9)
<i>Anurophorus binoculatus</i> (Kseneman)	1.432	1.171	0.984	(24)
<i>Dicyrtoma ornata</i> (Nicolet)	1.593	1.132	0.982	(18)
<i>Folsomia quadrioculata</i> (Tullberg)				
Juveniles	2.341	1.396	0.921	(24)
Adults	1.330	1.233	0.972	(24)
<i>Friesia mirabilis</i> (Tullberg)				
Juveniles	1.647	1.398	0.972	(24)
Adults	1.646	1.258	0.968	(24)
<i>Isotoma sensibilis</i> (Tullberg)				
Juveniles	3.592	1.732	0.955	(24)
Pale adult form	2.079	1.228	0.930	(20)
Dark adult form	1.706	1.313	0.952	(20)
Total adults	2.015	1.448	0.911	(24)
<i>Isotomiella minor</i> (Schäffer)	1.668	1.259	0.988	(24)
<i>Isotomurus palustris</i> (Müller)	5.128	1.500	0.958	(20)
<i>Lepidocyrtus curvicolis</i> Bourlet	1.881	1.201	0.984	(14)
<i>Neanura muscorum</i> (Templeton)	1.645	1.146	0.984	(14)
<i>Neelus minimus</i> Willem	1.403	1.119	0.993	(19)
<i>Onychiurus absoloni</i> (Börner)	1.737	1.452	0.961	(24)
<i>Onychiurus latus</i> Gisin	1.293	1.085	0.991	(20)
<i>Sminthurides pumilis</i> (Krausbauer)	2.107	1.166	0.950	(7)
<i>Tullbergia callipygos</i> Börner	1.716	1.450	0.978	(24)
<i>Willemia anophthalma</i> Börner	1.255	1.079	0.974	(20)

The species with the largest b value, *O. minimus*, is not predatory, whilst both *P. lapponicus* and *V. nemorensis* are predatory species and each of these have a value of b very close to unity.

Thus, if the value of b can be used as an index of the aggregation tendency, two general statements can be made about the Rannoch fauna. First, predatory species, although showing a heterogeneous distribution into aggregations, are less strongly aggregated than humus-, detritus- or fungus-feeding species. Secondly, the values of b are very similar for many species of Collembola and Cryptostigmata, and hence it would appear that the non-predatory species are showing about the same degree of tendency to aggregate.

By taking three-dimensionally contiguous soil samples, it was possible to investigate the size and distance relations of aggregations. By studying the statistic

$$\chi^2 = s^2(n-1)/m \quad (4.2)$$

Table 4.2. A comparison of the most frequently occurring species of Collembola, Cryptostigmata and Mesostigmata at Rannoch. In all cases adults and juveniles have been pooled to give total counts for the species.

Group and species	Total number extracted from all samples	Value of <i>b</i>
Collembola		
<i>Onychiurus asoloni</i>	7,146	1.452
<i>Isotoma sensibilis</i>	4,309	1.944
<i>Friesia mirabilis</i>	4,305	1.371
<i>Folsomia quadrioculata</i>	3,363	1.290
<i>Tullbergia callipygos</i>	1,995	1.716
Cryptostigmata		
<i>Tectocephus velatus</i>	12,165	1.571
<i>Platynothrus peltifer</i>	3,285	1.495
<i>Steganacarus magnus</i>	2,784	1.556
<i>Ceratoppia bipilis</i>	1,406	1.703
<i>Adoristes poppei</i>	1,358	1.623
Mesostigmata		
<i>Olodiscus minimus</i>	2,230	1.254
<i>Veigara nemorensis</i>	917	1.034
<i>Parazercon radiatus</i>	872	1.152
<i>Trachytes pyriformis</i>	726	1.181
<i>Pergamasus lapponicus</i>	497	1.019

where s^2 and m are defined above and n is the number of samples, Usher (1969, 1971a, 1975b) has recognized five types of spatial distribution, namely uniform (χ^2 significant with $p \geq 0.95$), random (χ^2 not significant), spatially large aggregations or 'gradients' (χ^2 significant with $p \leq 0.05$, and with an analysis of variance of the data for a block of samples showing significant differences between rows and/or columns), distinct aggregations (χ^2 significant with $p \leq 0.05$, but with no significant differences between rows and/or columns in the analysis of variance. Distinct aggregation can be seen by inspection of the data, as in Fig. 4.3), and other aggregations (significance as above, but distinct aggregations were not discernable in the data).

A summary of such analyses of the arthropods at Rannoch is given in Table 4.3. Comparisons of the various groups shows that a random distribution is more common in the Mesostigmata than in the Cryptostigmata and Collembola, and that a distribution into spatially large aggregations, the gradients, is less common in the Collembola than in the mites. A uniform distribution is particularly rare. As far as individual species are concerned, many of the Collembola (Usher 1969) and Cryptostigmata (Usher 1975b) occurred only in aggregations. The juveniles of both groups showed less

Table 4.3. A summary of the form of the distribution of the arthropods in the soil. The five types of distribution are discussed in the text. The data are presented for all species, and for the groups of five most frequent species listed in Table 4.2.

	Number of species included	Number of blocks of samples analysed	Distributions				
			Uniform	Random	Gradients	Distinct aggregations	Other aggregations
Collembola	12	234	2	64	9	121	38
	5 most frequent	198	2	49	9	103	35
Cryptostigmata	12	212	0	17	48	99	48
	5 most frequent	133	0	7	32	54	40
Mesostigmata	11	103	0	43	18	33	9
	5 most frequent	88	0	34	16	29	9

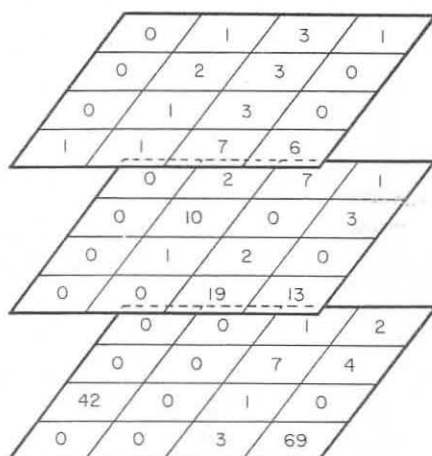


Figure 4.3. The distribution of juvenile *Isotoma sensibilis* in a block of samples collected in February. Large, distinct aggregations can be seen, particularly in the lowest layer where there are large isolated counts of 42 and 69.

tendency to occur at random than the adults. In the predatory Mesostigmata, although the tendency was towards randomness many species still exhibited a considerable degree of aggregation (for example *V. nemorensis* was aggregated in 13 of the 20 blocks analysed).

The aggregated distributions were further examined to determine the nature of the aggregation response. Amongst the Collembola the only species to occur more than once with a gradient type of aggregation was *O. absoloni*. It is perhaps a feature of this genus that they form territorially large aggregations (Glasgow 1939). Amongst the mites many species occurred in a gradient situation, and in *T. velatus* no 'distinct' aggregations were found by inspection of the data. Since these territorially large aggregations were demonstrated by a gradient across a block of samples, it can be seen that the size of the aggregation is at least the same as that of the block of samples, i.e. that such aggregations have a horizontal dimension of at least 250 cm².

The data of distinct aggregations can be subjected to further analysis. A block of samples with juvenile *I. sensibilis* is shown in Fig. 4.3, from which it can be seen that there are four aggregations. The analysis of the distinct aggregations was performed to determine the number of aggregations in a block of samples, the distance between aggregations (assuming that the arthropods were at the centre of the samples in which they occur), the distribution of the aggregations themselves, and the relation between population density and the aggregation response.

It is a feature of all three groups that the most frequently occurring

Table 4.4. The numbers of distinct aggregations formed in a block of samples. The data are given for the whole of a group and for the five* most frequently occurring species in the group as listed in Table 4.2.

	Number of aggregations in a block					Mean
	1	2	3	4	≥ 5	
Collembola, all species	14	31	45	19	13	2.94
Collembola, 5 species	7	25	32	17	12	3.10
Cryptostigmata, all species	33	34	18	11	3	2.16
Cryptostigmata, 4 species	10	21	13	7	3	2.48
Mesostigmata, all species	18	13	6	2	2	1.95
Mesostigmata, 5 species	12	10	3	2	2	2.04

*Only 4 species of Cryptostigmata since *T. velatus* did not occur as distinct aggregations.

species tend to have more aggregations per block of samples than the less frequently occurring species. The means in Table 4.4 indicate that the horizontal area occupied by an aggregation is about 80 cm² in the Collembola, about 100 cm² in the Cryptostigmata and of the order of 120 cm² in the Mesostigmata. However, these areas measure both the area of high density and the surrounding area of low density: visual inspection of the data indicated that whereas the area of high density was frequently in two or more adjacent samples in the Collembola and Cryptostigmata it was frequently confined to a single sample in the Mesostigmata. Thus, the horizontal size of the aggregation is often less than 20 cm² in the predatory species and frequently of the order of 30 to 50 cm² in the non-predatory species.

The distances between aggregations can be used to investigate the function of the aggregation response in these arthropods. First, if the distances between the centres of aggregation are less variable than would be expected at random and relatively large in length, then this might suggest that there is some form of aggregation territoriality (cf. Wynne-Edwards, 1962 for a general discussion of territoriality) whereby the group of arthropods and not the individual establishes a territory. Such a relation cannot, however, really be demonstrated in the soil arthropods. Usher (1969) indicated that uniformity of distance between aggregations occurred in the dark adult form of *I. sensibilis*, and the data are indicative of an approach towards uniformity in the pale adult form. Also *O. minimus* showed uniform spacing between aggregations (Usher 1971a) and there is an approach towards uniformity with the aggregations of adult *C. bipilis*.

Secondly, the distances between the centres might be rather irregular and bimodal, with a number of short distances and a number of long distances. Such a distribution is exhibited by the adults of *P. peltifer* and is indicative of aggregations being clustered together so that the aggregations are themselves aggregated. This form of distribution in the soil could be

an intermediate form of distribution between the territorially small distinct aggregation and the territorially large gradient, and might reflect local pockets of particularly high density in an area of generally high density. This doubly aggregated distribution is not particularly common, being shown only by *P. lapponicus* in the Mesostigmata and by the juveniles of the Collembola *I. sensibilis*, *F. mirabilis* and *F. quadrioculata*. The latter observation, relating to juveniles, might suggest that Collembola search out more favourable environments for the deposition of their eggs.

Thirdly, the distances between aggregations might be more or less random. This is an assumption of the negative binomial distribution, and hence it has been assumed by many soil biologists (e.g. Hartenstein 1961; Berthet & Gérard 1965; Gérard & Berthet 1966). However, the fact that the aggregations of most species are randomly scattered throughout the soil is likely to make the detection of causes of aggregations more difficult.

Finally, from the analysis of the distinct aggregations, the relation between aggregation tendency and population density can be investigated. Usher (1969) proposed three types of relation namely:

Type I, as the population density increases so does the number of aggregations per unit of surface area or volume. If r_n is the correlation coefficient between the population density and the number of aggregations, and r_s the correlation coefficient between the population density and the mean number of individuals in an aggregation, then for a Type I relation r_n would be positive and significant and r_s would be non-significant (or possibly negative);

Type II, as the population density increases so does the mean number of individuals per aggregation. Type II relations would be demonstrated if r_n was nonsignificant and r_s positive and significant;

Type III, is a composite of the previous two types, probably occurring if niches became unsuitable at high population densities. Type III relations would be demonstrated if both r_n and r_s were positive and significant (or possibly due to data shortage if neither were significant).

The results of analysis of the more common species are shown in Table 4.5. The Collembola and Mesostigmata, whenever the relation could be identified, showed a Type I response. Since this implies that more aggregations are being formed with increasing population density, it could be argued that the species in these groups have wide niches. Many species of Cryptostigmata had a Type II relation. Since this implies that new sites for aggregations are not being formed as the population density increases, these species might in general have relatively narrow niches. Type III relations, being intermediate between Types I and II, might thus occur with species with intermediate sized niches: the only species at Rannoch to show a Type III relation are the adults and juveniles of *P. peltifer*.

Table 4.5. The correlation coefficients between population density and the mean number of arthropods within distinct aggregations (r_s) and the number of aggregations (r_n), and the type of relation between population density and aggregation response. Only the most frequently occurring species are included. Levels of significance are indicated by n.s.—not significant, *— $0.01 < p \leq 0.05$, **— $0.001 < p \leq 0.01$ and ***— $0.001 \geq p$.

Species	Sample size	r_n	r_s	Type
Collembola				
<i>O. absoloni</i>	8	0.63 n.s.	-0.66 n.s.	I?
<i>I. sensibilis</i>				
Juvenile	23	0.63 ***	0.18 n.s.	I
Pale adult	17	0.65 **	0.40 n.s.	I
Dark adult	8	0.31 n.s.	-0.35 n.s.	?
<i>F. mirabilis</i>				
Juvenile	10	0.84 **	0.29 n.s.	I
Adult	8	0.53 n.s.	0.27 n.s.	?
<i>F. quadrioculata</i>				
Juvenile	14	0.49 n.s.	-0.22 n.s.	?
Adult	5	0.93 *	0.71 n.s.	I
<i>T. callipygos</i>	8	0.33 n.s.	-0.13 n.s.	?
Cryptostigmata				
<i>P. peltifer</i>				
Juvenile	10	0.78 **	0.53 n.s.	III?
Adult	8	0.84 **	0.85 **	III
<i>S. magnus</i>	5	-0.34 n.s.	0.73 n.s.	?
<i>C. bipilis</i>				
Juvenile	6	0.37 n.s.	-0.16 n.s.	?
Adult	14	0.18 n.s.	0.71 **	II
<i>A. poppei</i>	11	-0.17 n.s.	0.78 **	II
Mesostigmata				
<i>O. minimus</i>	6	0.34 n.s.	-0.29 n.s.	?
<i>V. nemorensis</i>	7	0.58 n.s.	0.16 n.s.	?
<i>P. radiatus</i>	5	0.89 *	0.78 n.s.	I
<i>T. pyriformis</i>	6	0.21 n.s.	-0.24 n.s.	?
<i>P. lapponicus</i>	5	-0.21 n.s.	-0.72 n.s.	?

The analyses of the individual species thus show that aggregations occur very frequently and that they are very heterogeneous in their size. The aggregation responses are partially determined on a seasonal basis, but more importantly there is a relation between the form of the aggregation and the population density. These analyses thus quantify the aggregation process, but they cannot determine the causes of aggregations.

INTERRELATIONS BETWEEN ARTHROPODS AND THE ENVIRONMENT

Correlation

For each of the 48 samples within a block there are counts of the numbers of each of the species of Collembola, Cryptostigmata and Mesostigmata and estimates or direct measurements of seven features of the environment. Since on each sampling date two blocks of samples, each located at random, were taken, a correlation coefficient can be estimated for the 96 samples. However, treating each sample as being randomly located might introduce an error, which has been eliminated by the following technique. For each block independently, an analysis of variance or analysis of covariance has been performed on each variate and on each pair of variates, removing the variance or covariance due to position (row or column) within the block. The correlation coefficient was calculated for the residual variances and covariance by the formula

$$r_{ij} = \frac{\text{residual covariance } (i, j)}{\sqrt{(\text{residual variance } (i) \times \text{residual variance } (j))}} \quad (4.3)$$

where i and j relate to any pair of variates ($i \neq j$), and the residual variances and covariances have 41 d.f. The r_{ij} s for both blocks of samples were transformed to z_{ij} by

$$z = 0.5 \ln \left(\frac{1+r}{1-r} \right) \quad (4.4)$$

the two values for z_{ij} averaged, and a pooled correlation coefficient calculated from

$$r = \frac{e^{2z} - 1}{e^{2z} + 1} \quad (4.5)$$

The effective number of degrees of freedom of such a pooled correlation coefficient is 78.

In order to illustrate the methods of analysis, the data for the Collembola and environmental features in samples collected on 16th January 1966 will be discussed (Table 4.6). Inspection of the correlation coefficients shows some of the relations between the Collembola and the environment: adult *F. mirabilis* is positively related to nitrogen content and *A. binoculatus* is negatively related to potassium content. These two relations might be real since the species show just the one relation and are not correlated to a complex of environmental features. However, the correlations of juvenile *F. quadrioculata* are positive for depth, water content and nitrogen, and negative

Table 4.6. The pooled correlation matrix, calculated from equations 4.3, 4.4 and 4.5, for the relation between the Collembola and the environmental features (data from samples collected 16 January 1966). For statistical significance, correlation coefficients would have to exceed in absolute value the .05, 0.29 ($p=0.01$) and 0.36 ($p=0.001$). Values that are statistically significant are set in bold type.

Variates	Variates																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. <i>F. mirabilis</i> (juv.)																		
2. <i>F. mirabilis</i> (ad.)	.32																	
3. <i>O. absoloni</i>	.16	.19																
4. <i>O. latus</i>	.07	-.02	.19															
5. <i>T. callipygos</i>	.28	.08	-.05	.18														
6. <i>A. binoculatus</i>	.01	-.14	.13	.14	.05													
7. <i>F. quadrioculata</i> (juv.)	.10	.18	.02	.01	.01	.11												
8. <i>F. quadrioculata</i> (ad.)	-.01	.07	.07	.26	-.10	.43	.11											
9. <i>I. minor</i>	.31	.27	.36	.12	0	.22	.18	.29										
10. <i>I. sensibilis</i> (juv.)	-.07	.13	.46	.32	.01	-.02	-.17	.05	.02									
11. <i>I. sensibilis</i> (pale ad.)	-.07	-.19	.35	.13	.04	.02	-.42	-.09	-.13	.31								
12. <i>I. sensibilis</i> (dark ad.)	-.11	-.03	.24	-.18	0	.04	-.20	-.22	-.10	.19	.60							
13. Depth	-.02	.16	-.41	-.21	-.02	.09	.44	-.06	.08	-.47	-.55	-.23						
14. Water content	-.04	.09	-.39	-.25	-.11	.11	.40	-.07	.18	-.48	-.57	-.25	.88					
15. Pore space	-.08	-.10	.44	.21	-.05	.04	-.34	.07	-.01	.43	.54	.29	-.89	-.67				
16. Nitrogen	.12	.32	-.19	-.11	.16	-.19	.22	-.17	-.09	-.23	-.14	-.09	.44	.29	-.47			
17. Phosphorus	-.01	.10	.48	.27	.05	-.04	-.28	.13	-.02	.49	.54	.22	-.74	-.73	.68	-.14		
18. Potassium	.09	-.13	.20	.04	-.12	-.30	-.36	-.08	-.13	.24	.48	.16	-.76	-.73	.55	-.28	.56	
19. Calcium	.14	.12	.29	.20	-.03	-.21	-.27	-.08	-.12	.28	.39	.03	-.53	-.61	.48	-.03	.61	.42

for pore space, phosphorus, potassium and calcium. The positive and negative correlations are reversed for juvenile *I. sensibilis*. Inspection of the correlations between the environmental features shows that strong correlations exist, particularly between depth, water content and pore space. The main problem with interpreting data such as in Table 4.6 is the concept of 'cause and effect'. If, for example, any species correlates positively with depth, then it can be predicted (i) that there would be a positive correlation with water content (r between water and depth is 0.88) and (ii) that there would be a negative correlation with pore space (r between depth and pore space is -0.89). Such a pattern of correlations can be seen in the data, and it is thus impossible to say whether the number of individuals can be attributed to either depth, water content or pore space. There are, therefore, in the environmental data complexes of highly correlated influences acting either singly or together on the arthropods. Calculation of partial correlation coefficients, as undertaken by Poole (1961, 1962), is generally not very helpful when the environmental influences are so strongly correlated: for example, if the partial correlation coefficient between juvenile *I. sensibilis* and each of the three environmental features, depth, water content and pore space are calculated (Table 4.7), only one of the coefficients is significant

Table 4.7. Correlation and partial correlation coefficients for the relation between the juveniles of *I. sensibilis* and the three environmental features, depth, water content and pore space. In the table the following notation has been used: *I*, *Isotoma*; *W*, water content; *D*, depth; and *P*, pore space; and a dot in a list of subscripts implies that variates after the dot have been eliminated.

Correlation coefficients	Partial correlation coefficients	
$r_{IW} = -0.48$	$r_{IW.D} = -0.16$	$r_{IW.DP} = -0.20$
	$r_{IW.P} = -0.29$	
$r_{ID} = -0.47$	$r_{ID.W} = -0.11$	$r_{ID.PW} = 0.05$
	$r_{ID.P} = -0.21$	
$r_{IP} = 0.43$	$r_{IP.W} = 0.17$	$r_{IP.DW} = 0.13$
	$r_{IP.D} = 0.03$	
$r_{WD} = 0.88$	$r_{WD.P} = 0.84$	
$r_{WP} = -0.67$	$r_{WP.D} = 0.52$	
$r_{DP} = -0.89$	$r_{DP.W} = -0.85$	

after elimination of one feature ($r_{IW.P}$ in Table 4.7), and none of the correlations are significant after elimination of two features.

Such results with matrices of correlation coefficients or partial correlation coefficients indicate the need for analysis by some method that can demonstrate the combined effects of several variables.

Factor and principal component analysis

In a multivariate situation one is concerned with a set of m variates, which might include numbers of species and environmental features, each of which has been recorded in n samples. If a variate is denoted by X_i ($i=1, 2, \dots, m$), then the basic model of factor analysis is

$$X_i = \sum_{r=1}^k l_{ir} f_r + e_i \quad (4.6)$$

where there are k ($k < m$) common factors f_r , l_{ir} are the factor loadings, and e_i represent a residual source of variation, the unique variances.

Ecologically, the factor analysis model thus states that the individual biological attributes of such a multivariate system can be expressed in terms of a small number, k , of common factors and a residual unique source of variation. The analysis estimates values of l_{ir} and e_i , and aims to interpret the meaning of these common factors. Although the model is not based on any hypothesis about the distribution of the variables x_{ij} , in the data matrix, the use of the product moment correlation coefficient, the techniques of maximum likelihood estimation (Lawley & Maxwell 1971; Jöreskog 1967; Jöreskog & Lawley 1968) and the testing of significance do require that the variables x_{ij} are drawn from a multivariate normal distribution. Since this is not the case with counts of soil arthropods, logarithmic transformation of the data has been used. Also, in biological situations the assumption of linearity of the common factors is often doubtful, but it suffices as a first approximation. Correlation matrices have been used in preference to covariance matrices since they eliminated the problems of scaling of the original variates (which would have been impossible in data where some of the variates are counts of animals and other variates are measures of the environment). The computer programme referred to by Jöreskog (1967) has been used for the estimation of all factor loadings and unique variances quoted in this paper.

The factor analysis model can be compared with principal component analysis, which transforms the m variates X_i into a set of m uncorrelated variates Y_i according to the following rule. Y_1 has a maximum possible variance, Y_2 has a maximum variance subject to being uncorrelated with Y_1 (i.e. orthogonal axes), Y_3 has a maximum variance subject to being uncorrelated with Y_1 and Y_2 , and so on. Principal component analysis can thus be represented by

$$X_i = \sum_{r=1}^m l_{ir} Y_r \quad (4.7)$$

where l_{ir} are the loadings. The ease of the principal component model lies in the fact that the loadings are given by the latent vectors of the correlation matrix \mathbf{R} , and the variance accounted for by each new variate, Y_r , is given by the ratio of the appropriate latent root of \mathbf{R} to the trace of \mathbf{R} .

A principal component analysis of the data in Table 4.6, extended to include the mites, is shown in Figs. 4.4 and 4.5. The first component accounts for over 30% of the variance, and is clearly much larger than the

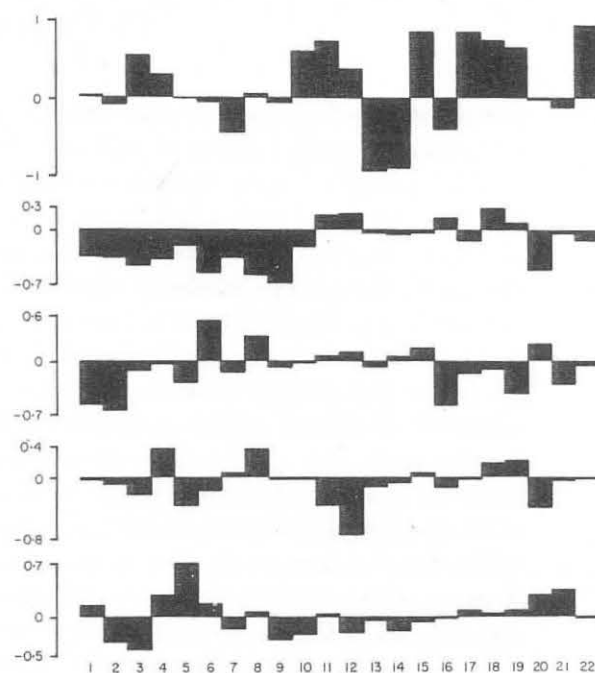


Figure 4.4. The loadings on the first five principal components for the samples collected on 16 January 1966. The numbers relate to the species and environmental features listed in Table 4.6, except that three additional variates have been added (20—the predatory Mesostigmata, 21—the non-predatory Mesostigmata (genera *Olodiscus*, *Zercon*, *Parazercon* and *Trachytes*) and 22—the Cryptostigmata).

remaining components (Table 4.8). The loadings, Fig. 4.4, indicate that the group of three environmental features, depth, water content and pore space, are important in interpreting this component since the first two are large

Table 4.8. A principal component analysis of the data in Table 4.6, extended to include the mites.

Component	1	2	3	4	5
Latent root	6.64	2.47	1.95	1.46	1.32
Percentage of variance	30.2	11.2	8.8	6.6	6.0

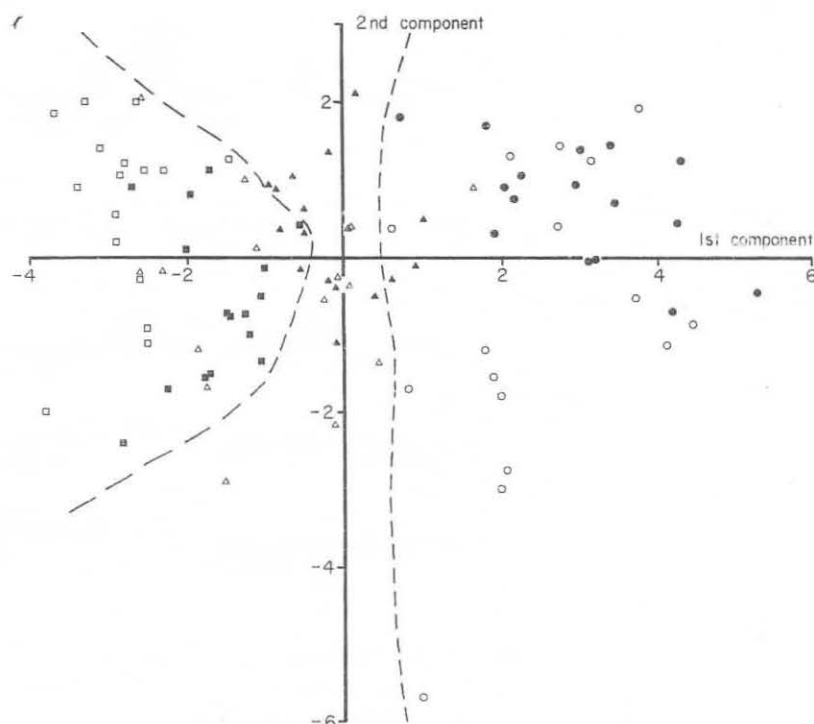


Figure 4.5. The first two principal components, derived from the data in Table 4.6 and Fig. 4.4. Circles represent samples from the surface layer, triangles from the centre layer and squares from the lowest layer. Open symbols relate to one block of samples, filled symbols to the other block of samples. The two dashed lines delimit the rightward extent of square symbols and the leftward extent of the circle symbols.

and negative and the third is positive. The second component is of interest, since all the environmental variates have near-zero loadings, whilst the majority of species of Collembola and the predatory Mesostigmata have large (negative) loadings. Although this component accounts for only little more than 11% of the variance, it would appear to be related to some general sociability of the soil arthropods. The remaining components in Fig. 4.4 all account for rather small percentages of the variance, and from a single analysis their interpretation is uncertain, except in so far as the loading for nitrogen in the third component is reasonably large. Plotting the first two components, whose interpretation is straightforward, produces a scatter of points without any clearly defined clusters (Fig. 4.5). The increase in depth from right to left in Fig. 4.5 makes it clear that, ecologically, the surface and lowest layers of the soil are distinct, since there is no overlapping of samples from these two layers. It would therefore appear that the arthropod community of the surface litter horizon is different from the community of the fermentation horizon.

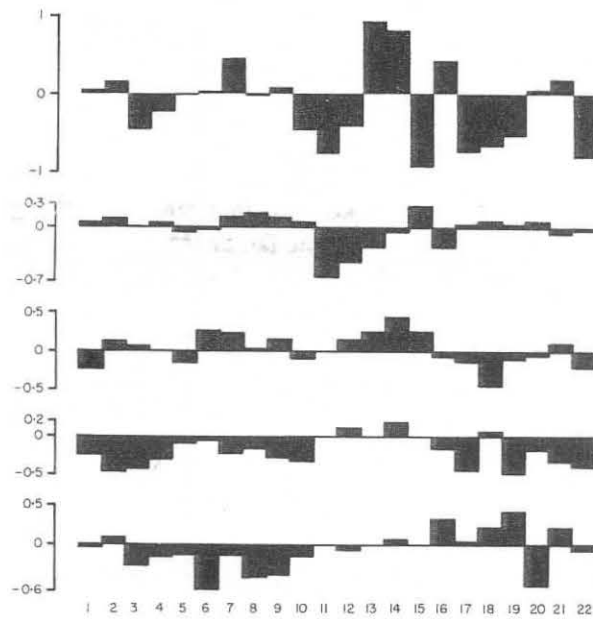


Figure 4.6. The loadings of five common factors derived from the correlation matrix in Table 4.6. The numbers relate to species and environment features and are listed in Tables 4.6 and 4.9, extended as in Fig. 4.4.

Maximum likelihood factor analysis indicated that five common factors were sufficient to account for the covariance in the data. The loadings are shown in Fig. 4.6 and the unique variances in Table 4.9. The unique variances for depth and pore space are zero since all of their variation has been

Table 4.9. The unique variances derived from a factor analysis of the data in Table 4.6, extended to include the mites.

Species	Unique variance	Environmental feature	Unique variance
1. <i>F. mirabilis</i> (juv.)	·78	13. Depth	0
2. <i>F. mirabilis</i> (ad.)	·33	14. Water content	·11
3. <i>O. absoloni</i>	·50	15. Pore space	0
4. <i>O. latus</i>	·72	16. Nitrogen	·58
5. <i>T. callipygos</i>	·95	17. Phosphorus	·25
6. <i>A. binoculatus</i>	·54	18. Potassium	·30
7. <i>F. quadrioculata</i> (juv.)	·70	19. Calcium	·25
8. <i>F. quadrioculata</i> (ad.)	·69	20. Predatory	
9. <i>I. minor</i>	·62	Mesostigmata	·71
10. <i>I. sensibilis</i> (juv.)	·64	21. Non-predatory	
11. <i>I. sensibilis</i> (pale ad.)	·26	Mesostigmata	·81
12. <i>I. sensibilis</i> (dark ad.)	·22	22. Cryptostigmata	·13

accounted for by the five common factors. The unique variances of the other environmental features are generally small, indicating that their distribution is accounted for reasonably well by the five common factors. The Collembola are variable: whereas the adults of *F. mirabilis* and *I. sensibilis* have small unique variances, other species, particularly *T. callipygos*, have large unique variances. Unlike principal component analysis, where the components could be ordered, the factors form a set of five that cannot be ordered into the largest, etc. However, rotation of the factors is possible, and one such

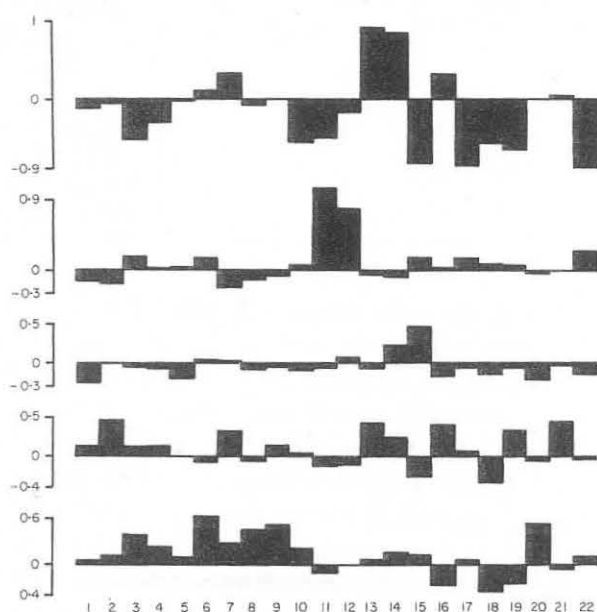


Figure 4.7. The same loadings as in Fig. 4.6 after rotation of the common factors by the Varimax method. The numbers relate to the same variates as in Fig. 4.6.

rotation by the widely-used Varimax method is shown in Fig. 4.7. This method of rotation has the general characteristic of increasing the size of a few of the loadings, whilst making many more loadings near zero, and thus aiding the interpretation of the factors.

Interpretation

The number of principal component and factor loadings shown in Figs. 4.4 and 4.6 is limited for ease of presentation, but there is no limit to the size of matrix analysed except that imposed by the computer store available. The unique variances for species in the two groups of mites, Mesostigmata and Cryptostigmata, are listed in Table 4.10. Comparing each group of vari-

Table 4.10. The unique variances for factor analyses of the Mesostigmata and Cryptostigmata data collected on 16 January 1966.

Mesostigmata species	Unique variance	Cryptostigmata species	Unique variance
<i>O. minimus</i>	·78	<i>T. velatus</i>	·02
<i>V. nemorensis</i>	·91	<i>P. peltifer</i>	
<i>P. radiatus</i>	·87	Juvenile	·59
<i>T. pyriformis</i>	·92	Adult	·44
Juvenile <i>Zercon</i> , etc.	·78	<i>S. magnus</i>	·52
<i>Eugamasus</i> sp.	·69	<i>C. bipilis</i>	
		Juvenile	·30
		Adult	·14
		<i>A. poppei</i>	·23
		<i>Chamobates schützi</i>	·68
		<i>Eupelops</i> sp.	·45
		<i>Camisia spinifer</i>	·30
		<i>Porobelba spinosa</i>	·80

ates, the mean unique variance of the Mesostigmata is 0·82, of the Collembola 0·58, of the Cryptostigmata 0·41, and of the seven environmental features 0·21. These means indicate that the factor analysis model is giving a reasonably good fit to the Cryptostigmata data since the unique variances are generally reasonably small and the common factors account for a large amount of the correlation. In the Mesostigmata data the common factors are accounting for very little of the observed correlation, whilst the Collembola are intermediate between the Cryptostigmata and Mesostigmata. The environmental features have generally small loadings indicating that the common factors can be interpreted in terms of environmental influences.

Since blocks of samples were collected on twelve occasions during the year, some general statements can be made about the interpretation of the principal component and factor loadings. In all instances the principal component accounting for the largest amount of the variance, as well as one of the factors, is structural, showing large loadings on depth and water content, and a large contrary loading on pore space. In all instances this factor or component reflects the vertical distribution of the species, separating the species of the soil surface (often large species such as adult *I. sensibilis*, *Tomocerus minor*, *A. poppei* and *C. bipilis*) from the species occurring deeper in the soil (such as *T. calipygos* or the juveniles of *F. quadrioculata*). Since this first factor is concerned with the vertical distribution of the microarthropods, it contains relatively little information concerning the causes of aggregation except in so far as specifying the depth at which most aggregations are likely to occur.

In the majority of analyses three other factors or components could be

interpreted. First, one of these is associated with the general 'sociability' of the species, since large loadings of the same sign were found with the majority of species of Collembola and mites, and the loadings on the environmental features were small. This factor indicates that when arthropods are frequent, many species contribute to this abundance, or conversely that the majority of species tend to avoid some area. Since the environmental features have near zero loadings on this factor, the cause of this general sociability cannot be investigated.

Secondly, a factor relating to nitrogen was frequently seen in the analysis. In this factor the loading on the nitrogen content was large whilst the loadings on other environmental features were small (except sometimes phosphorus and calcium which also showed large loadings). Amongst the arthropods, *C. spinifer*, *F. mirabilis* and *O. absoloni* (summer months only), showed large loadings, though at some seasons of the year many other species had large loadings on this factor. The interpretation of this factor ecologically is more difficult: nitrogen has been shown to occur in rather small 'concentration aggregations'. However, a likely explanation is that high nitrogen content is related to faecal content. If this is correct, this factor might suggest aggregations where the arthropods are living and defaecating (a trivial result) or it might suggest aggregation at sites of former biological activity. The association with this factor of *F. mirabilis*, or species with sucking mouthparts and no visible gut contents, suggests possibly the latter since arthropod faeces are known to be good substrates for microbial activity.

Thirdly, a factor relating to potassium content was frequently seen in the analysis. In this factor the loading on the potassium content was large whilst the loadings on other environmental features, except calcium on occasions, were small. Rather few species of arthropods had large loadings, though *O. absoloni* (autumn and winter only) and *P. peltifer* had loadings of the same sign as potassium and adult *I. sensibilis* tended to have loadings of the contrary sign. Ecologically, the potassium content might be a reflection of the active roots or mycorrhiza in the soil. The 'concentration aggregations' of potassium were larger than those of nitrogen, and would approach the volume occupied by a surface feeding root of a pine tree. Tentatively, then, this factor can be interpreted in relation to the rhizosphere.

The interpretation of the factor analyses thus indicates four influences acting upon the community of soil arthropods. These relate to the vertical distribution of the individual species, to the general sociability of the species, and tentatively to the sites of former biological activity and the rhizosphere. When Collembola were examined, a fifth factor could sometimes be seen: this related to the predatory species of the Mesostigmata, which tended to show negative loadings with species of the family Onychiuridae and positive loadings with species of Isotomidae. Harris (1975) has demonstrated that

Pergamasus longicornis will eat Isotomids in preference to Onychiurids. This factor thus does not relate to the causes of aggregation, but rather to the fact that predatory species tend to be distributed in relation to their preferred prey species.

Discussion

Studies on aggregation or pattern of species are interesting for two reasons. First, is there any biological significance in the clumping together of individuals, or is it merely an accident of the biology of the species concerned (such as, for example, an aggregation of juveniles at the site of an egg cluster)? Secondly, does the formation and causation of aggregations throw any light on the co-existence within a limited area of a number of species that appear to be ecologically similar?

The nature of the clumping together of individuals may indicate the biological significance of the aggregation process. Five types of pattern have been described by Hutchinson (1953), who named them:

Vectorial—the distribution is determined by external influences, such as temperature, humidity, density gradients, winds, etc.

Reproductive—the distribution may be determined by the offspring remaining near the parents.

Social—the distribution is determined by signalling of various kinds, leading either to spacing or clumping.

Coactive—the distribution may be determined by interaction between species in competition.

Stochastic—the distribution is determined by random forces.

There are a considerable number of studies of pattern in plant populations, and these tend to show that small-scale pattern is reproductive, due to vegetative spread of species and limited seed dispersal, and larger-scale pattern is vectorial being imposed on the vegetation by the pattern of the environment. In studies of soil arthropods, any one of these five categories of pattern may occur, though aggregations are likely to result only from the first four listed. Hale (1966) suggested that aggregations could be explained by a slow dispersion from the site of an egg cluster (reproductive pattern) and by a coming together at a food source (vectorial pattern). Laboratory observations on the behaviour of juvenile *Isotoma sensibilis*, remaining at the egg cluster site for three instars before dispersing (Usher 1969), suggest that reproductive pattern is frequent amongst juveniles, though such a pattern could not exist in the predatory Mesostigmata which lay single eggs apparently at random (Harris 1975). A change from reproductive to other forms of pattern over the life span of a soil arthropod seems likely (Takeda 1973; Barra & Christiansen 1975).

The majority of laboratory and field studies indicate that aggregation in adults is vectorial pattern. This is particularly clearly shown by Joosse's (1966) study of *Anurida maritima*, which is stimulated to aggregate in air-filled crevices either by the incoming tide or by rain at low tide. Whatever the vectorial influence, it would appear that an ability to respond to this influence is important for the survival of the individual since it will be forced into a micro-environment in which its chances of survival are greater than in any random micro-environment. Thus, aggregation allows a species to achieve a larger population density than if it were not aggregated. Studies at Rannoch have shown that the more frequent species of Collembola and Cryptostigmata tend to be more strongly aggregated than the rarer species: the values of b in Table 4.1 are correlated with the overall abundance of the Collembola, ($r=0.57$, 17 d.f., $p=0.01$). A similar correlation with the Cryptostigmata fails to be significant ($r=0.44$, 14 d.f., $p>0.05$). The data from Rannoch therefore tend to support the hypothesis that an aggregated species can maintain a greater population density than a non-aggregated or weakly aggregated species. Improved methods in estimating the tendency to aggregate (Patil & Stiteler 1974) might be useful in proving or disproving this hypothesis.

Social and coactive patterns are much more difficult to demonstrate under field or laboratory conditions due to correlation between any features of the system that are measured. Observations on moulting groups of Collembola (Strebel 1932) suggest that in this instance social aggregations are transitory, and have some protective function for the moulting Collembola. Strebel demonstrated this form of aggregation for *Hypogastrura purpurascens*. Harris (1975) has shown that predatory mites find this genus distasteful, and B.C. Longstaff claims (personal communication) to be able to detect an unpleasant smell in high density cultures of *H. denticulata*. Joosse (1970, 1971) has suggested that aggregations of Collembola that have no courtship behaviour are essentially vectorial, but that they have an important social role since they increase the chance of females making contact with spermatophores. Thus the location of the aggregation is vectorial although the stimulus is social. In the Rannoch data the species with courtship behaviour are infrequent, and hence the data cannot be used to test Joosse's hypothesis. There are no field or laboratory studies in which coactive pattern in soil arthropods has been demonstrated. Such a pattern is very difficult to prove under field conditions where two species might appear to have separate and clearly distinct niches although this might be due to inter-specific competition forcing one of the species out of its optimal niche. Coactive patterns in soil arthropods can really only be proved in controlled laboratory experiments.

The different niches occupied by soil arthropods at first sight seem hard

to enumerate. There is perhaps a conflict in the methods of analysis used. If a multivariate approach is selected (Bonnet *et al.* 1970; Hill 1971) then the fundamental idea is to explain the distribution of several species in terms of a few environmental factors or components. If, however, one assumes that there must be the same number or more niches or resources than species (Levins 1968), then a multivariate approach can only be inappropriate since one wants to increase and not decrease the influences to be considered. Blackith (1974) undertook such an analysis for the Collembola of Irish blanket bogs, but he had to make many assumptions which might be questioned.

The concept of the niche width of individual species may explain the observed relations between aggregation and population density listed in Table 4.5, where relations in the sequence I, III, II indicate a decreasing width of the species niche. The majority of species of Collembola and Mesostigmata had a type I relation (as population density increases so does the number of aggregations), whilst many of the Cryptostigmata showed a type II relation (as population density increases so does the number of individuals within an aggregation). *Folsomia candida*, which occurs in Britain in rather specialized habitats like greenhouses, has a type III relation (Usher & Hider 1975). These observations suggest that the niche widths of soil arthropods are variable. Investigation of multivariate data by factor analysis provides a series of k common factors and m unique variances, and is thus more realistic in the assessment of niches since there are $m+k$ possible niches determined by the analysis. The Collembola data, Fig. 4.6 and Table 4.9, indicate that although the 5 common factors have some effect on the community, each species also has a relatively large unique variance. An interpretation of factor analysis could be that the species own niche is represented by its unique variance, and that the overlap of niches is represented by the common factors. All the species of Collembola (Table 4.9) and mites (Table 4.10) thus show that there is some overlap of niches. These results are in accord with the conceptual framework on niches described by May (1974). The soil environment, particularly under a forest canopy as at Rannoch or in the Irish blanket bogs (Blackith 1974) is extremely steady, so there is an effective limit to niche overlap. Blackith invoked the environmental stability to explain the large proportion of pale coloured species, indicating that the observed proportion placed the Irish bogs in the tropics (by applying Gloger's rule). The soil environment is thus, for temperate climates, extremely steady. To quote May 'In a perfectly stable deterministic environment, arbitrarily close packing and rich speciation is possible, and to a certain limited extent the greater the environmental steadiness, the closer the packing, and the richer the consequent assembly of species.' It would therefore appear that environmental stability and aggregation behaviour promote a

large population density of an apparently large number of species in the superficially homogeneous soil environment.

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